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Individual differences in working memory and general intelligence indexed by P200 and P300: A latent variable model

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Highlights:

- The central executive system and short-term storage of a multi-component model of working memory were examined.
- The central executive system is thought to contain shifting, inhibition, and updating functions. The short-term storage is thought to contain the phonological loop and visuospatial sketchpad.
- Only the inhibition and updating functions were significantly related to general intelligence (*g*). The relationship between the central executive system and *g* was mediated by a 3-back P300 (mean amplitude for target stimuli) at the Pz electrode.
- The combined components of working memory predicted 60.4% of the variance in *g*, 65.7% in crystalized intelligence, and 62.7% in fluid intelligence.

Abstract

A robust relationship between working memory (WM) and general intelligence (*g*) has been well established. Nevertheless, explanations for this relationship in terms of underlying neurocognitive processes are still inadequate. This study addresses this issue using an individual differences approach in which Central Executive System (CES) and Short-Term Storage (STS) components of WM are measured comprehensively and examined for their

relationship with *g* via event-related potentials components (P200 and P300) as mediators. Participants (n=115) completed tests of the WM, CES and STS, as well as *g*. P200 and P300 components were recorded during 3-back WM task performance. Structural equation modelling showed significant negative associations between the P200 latency for target stimuli and CES shifting processes, and between the P300 amplitude for target stimuli and CES inhibition and updating processes. The relationship between CES processes and *g* was mediated in a localized fashion by the P300 amplitude. These findings further support the notion that the CES has a multidimensional structure and, importantly, reveal that the inhibition and updating functions of the CES are crucial in explaining the relationship between WM and *g*. Negative relations between ERP indices (P200 latency and P300 amplitude for target stimuli) and *g* support a neural efficiency hypothesis related to high intelligence.

Keywords: Working memory, Central executive system, Short-term storage systems, Event-related potentials, Structural equation modelling, Neural efficiency hypothesis

1. Introduction

Working memory (WM) has long been regarded as a multiple component construct in which a set of subsidiary storage modules are coordinated by a central mechanism, often referred to as the Central Executive System (CES; Baddeley and Hitch Working Memory Model; Baddeley, 2007; 2012; Baddeley & Logie, 1999; Cowan, 2005). Short-Term Storage (STS) is achieved by subsidiary mechanisms that 'automatically' retain and process information in a temporary fashion. These include, for example, the hypothesized phonological loop, which maintains verbal information, and the visuospatial sketchpad, which stores visual and spatial material (Baddeley, 2012). Although this established model concerning WM model has been widely accepted, it has been recognized that the CES construct is the most complex system of WM (Baddeley, 2012) with the need for clarity concerning its specific functions (Atkinson et al., 2018; Baddeley, 1996).

According to Miyake and colleagues (2000), there is also a general set of correlated, but separable, executive functions (EFs) related to WM that mirror those attributed to the CES, including: (1) 'Inhibition' of prepotent/ automatic responses, (2) 'Updating' of WM representation by monitoring and replacing old/ irrelevant information with newer/ more relevant information, and (3) 'Shifting' attention back and forth between concurrent tasks, operations and different mental sets in a flexible fashion. The functional comparability between a multidimensional CES and EFs is now well supported (Coolidge, Wynn, and Overmann, 2013; Dehn, 2014; Logie, 2011) and a strong relationship between these two constructs (r = 0.97) indicates a shared common variance (McCabe, Roediger, McDaniel, Balota, and Hambrick, 2010). The finding from previous studies showed that EF and the CES have been considered approximately synonymous and EF is significantly related to STS and predicts *g* as

well (Wongupparaj, Kumari, & Morris, 2015a, 2015b). Consequentially, the terms CES and EF are used interchangeably throughout the article.

The key contribution of the WM system to general cognition is reflected in the finding that WM task performance predicts individual differences in general intelligence (*g*), including such higher-order cognitive functions as reasoning and comprehension (Colom, Abad, Quiroga, Shih, & Flores-Mendoza, 2008; Engle, Tuholski, Laughlin, & Conway, 1999; Kane, Hambrick, & Conway, 2005; Unsworth, Fukuda, Awh, & Vogel, 2014). Studies have tended to support the notion that the efficiency of CES processes for attentional control and related EFs are the strongest candidates for explaining the link between WM and *g* (Burgess, Gray, Conway, & Braver, 2011; Engle & Kane, 2004; Engle et al., 1999; Friedman et al., 2006; Gray et al., 2017; Santarnecchi, Emmendorfer, Pascual-Leone, 2017). The ability of CES to predict *g* can be explained in terms of the extent to which the system can efficiently prioritize and sustain internal information during WM processing in which the CES acts in multiple steps to orient, select, inhibit, and reconfigure several representations when processing incoming information. This view suggests a major role in WM for the CES, whilst STS may be less involved (Myers, Stokes, & Nobre, 2017). Other studies, however, have found that encoding, maintenance, retrieval or rehearsal strategies - associated with STS – are specifically and solely linked to *g* (Cohen & Sandberg, 1977; Colom, Flores-Mendoza, Quiroga, & Privado, 2005; Martinez et al., 2011; Chuderski, Taraday, Necka, & Smolen, 2012; Shahabi, Abad, & Colom, 2014; Dang, Braeken, Colom, Ferrer, & Liu, 2014, 2015; Gignac, Shankaralingam, Walker, & Kilpatrick, 2016). It is possible that the CES and STS components are interrelated, but maintain independent contributions when explaining the variances in different kinds of intelligence, including fluid (*gF*; Logie & Duff, 2007; Unsworth et al., 2014; Unsworth et al., 2009; Song

& Jinyu, 2017), and crystallized intelligence (*gC*; Dang, Braeken, Colom, Ferrer, & Liu, 2013; Martínez et al., 2011), or both (Kuhn, 2016; Wongupparaj, Kumari, & Morris, 2015).

Although many studies have documented a substantial relationship among CES, STS, and *g* across populations using psychometric methods, the nature of this relationship remains unclear. Further understanding may be obtained if, as well as cognitive processes, the underlying neural processes are considered, for example, by using Event Related Potentials (ERPs; Corr, 2010; Euler, McKinney, Schryver, & Okabe, 2017). ERPs reflect electroencephalographic activity that is time-locked to stimulus presentation or a behavioural response, and is often measured by the amplitude and/or latency (post-stimulus time of occurance) of specific components (e.g., P200, P300) (Luck, 2014). Amplitude is proposed to reflect synchronized allocation of neural resources and power (Polich, 2007; van Dinteren, Arns, Jongsma, & Kessels, 2014), while latency indexes neural efficiency and speed. Early and late ERPs have been associated with individual differences in *g* (Federico, 1984; Haier, Robinson, Braden, & Williams, 1983; Jensen, 1999),

The fronto-central P200 occurs with a latency around 200 ms, and is proposed to reflect processes involved in selective attention (Hillyard, Hink, Schwent, & Picton, 1973), executive attention (Zhao, Zhou, & Fu, 2013), stimulus classification (García-Larrea, Lukaszewicz, & Mauguiére, 1992), STS (Dunn, Dunn, Languis, & Andrews, 1998) and intelligence (Lijffijt et al., 2009). The P300 component elicited at approximately 300ms post-stimulus by WM tasks (e.g., n-back) is proposed to index brain activities underlying fundamental attention, context updating and cognitive control processes (Scharinger, Soutschek, Schubert, & Gerjets, 2017; Sumich et al., 2008; Polich, 2007; Watter, Geffen, & Geffen, 2001). Some evidence suggests that *gF* and *gC* may be differentially related to P200 (earlier processes, Lijffijt et al., 2009)

and P300 (later processes, Amin et al., 2015; De Pascalis, Varriale, & Matteoli, 2008; Otsuka, Sunaga, Nagashima, & Kuroume, 1993; Russo, De Pascalis, Varriale, & Barratt, 2008) respectively. P200 and P300 have been shown to be related to active maintenance processes and interference phenomena during WM updating (Vilà-Balló et al., 2018). However, strong correlations and shared variance between these components mean that their independent contributions to WM and *g* remain unclear and the nature of the relationship between ERPs, WM and *g* has been elusive (Pahor & Jaušovec, 2017).

The neural efficiency hypothesis suggests that more intelligent (higher *g*) individuals use cognitive power and resources more efficiently, resulting in decreased activation of regions and networks (Neubauer & Fink, 2009). For example, reduction in glucose metabolism during learning of a visuospatial task is proportional to *g* (Haier, Siegel, Tang, Abel, & Buchsbaum, 1992). Developmental studies of ERPs, including P300, report a decrease in amplitude between adolescence and young adulthood, in parallel to protracted development of frontal networks (Sumich et al., 2012). However, it is unclear whether such reduction reflects neural degeneration or neural efficiency. Likewise, applicability of the neural efficiency hypothesis to the relationship between ERPS, WM and *g* remains controversial, with some authors reporting lower P300 amplitudes and others higher P300 amplitudes in high performers (Haier et al., 1988; Neubauer & Fink, 2009; Nussbaumer, Grabner, & Stern, 2015). Clarification of relationships between ERPS, WM and *g* requires better understanding of shared variance between factors and identification of more direct associations.

The present study uses Structural Equation Modelling (SEM) to investigate a multi-dimensional EF framework (Miyake and colleagues 2000; 2006) to predict *g*, which integrates behavioural measurement of WM components and mediating neurophysiological signals

(P200, P300). Specifically, three research hypotheses are tested: 1) CES and STS components predict *g*; 2) CES and STS components predict *g* via behavioral WM and neuronal WM (P200/ 300) mediators; and 3) if the neural efficiency hypothesis is correct, negative correlations will be found between the CES and STS components and neuronal WM data (P200/300), and between the neuronal WM data (P200/300) and *g*.

2. Methods

2.1. Participants and design

To ensure acceptable power in SEM, at least one hundred participants were required (Hair Jr., Black, Babin, & Anderson, 2009; Sideridis, Simos, Papanicolaou, & Fletcher, 2014). Thus, one hundred and fifteen participants (age range=18-44 years; M age = 25.74 years, SD age= 5.17; 76 female, 59.6% White, 67.9% with English as their native language) were recruited via the King's College London (KCL) circular email, Experimatch, and Facebook pages. As per our inclusion/exclusion criteria, all participants were required to: i) be right-handed based on the Edinburgh Handedness Inventory (Oldfield, 1971), ii) have normal hearing and corrected-to-normal vision, iii) not have a history of neurological or significant psychiatric disorders (e.g., history of depression or psychosis), and iv) not be on any medication affecting mental functioning.

For the purposes of initial analysis, the participants were divided into three groups based on their IQ scores (Wechsler, 2011): average (92-109), high average (110-120), and superior-to-very superior (121-147). *g* was split into crystallized and fluid components (*gC* and *gF*). The banding of the three groups followed the Wechsler banding approach (Wechsler, 2011), with the banding ranges approximately weighting the group sizes according to a normal distribution. The average to very superior range reflects the use of a primarily university student sample .

The study was approved by KCL Psychiatry, Nursing and Midwifery Research Ethics Subcommittee (PNM RESC/PNM/12/13-84). Participants provided written informed consent to their participation and received a reimbursement of £25 plus travel costs for participation.

2.2. Behavioral and ERP Measures

2.2.1. CES

For CES measurement, three standardized tasks reflecting the three CES functions identified in the Miyake and colleagues' (2000) framework were used. These included (1) inhibition, measured using a flanker task (adapted from Liu, Xiao, Shi, Zhao, & Liu, 2011) ($\alpha = 0.83$) with the overall response accuracy as the primary dependent measure; (2) updating, measured using an alpha span task (Schmiedek, Hildebrandt, Lövdén, Wilhelm, & Lindenberger, 2009) ($\alpha = 0.81$) with overall response accuracy as the primary dependent measure; and (3) shifting, measured using a computerized version of the Wisconsin Card Sorting Test (WCST) (computerized version from PEBL test battery version 0.14, Mueller & Piper, 2014) ($\alpha = 0.75$) with the total response error as the primary dependent measure (see Supplementary Material for detailed task descriptions).

2.2.2. STS

Regarding STS, the phonological loop was assessed using the forward digit span ($\alpha = 0.84$), and the visuospatial scratchpad was assessed using Corsi-block span tasks (computerized version from PEBL test battery version 0.14, Mueller & Piper, 2014), with the total number of individual items correct as the primary variables. Finally, intelligence measurement was derived from two subtests (Vocabulary, $\alpha = 0.78$ and Matrix Reasoning, $\alpha = 0.88$) of the

Wechsler Abbreviated Scale of Intelligence – second edition (WASI-II); respectively assessing *gC*, and *gF* (Wechsler, 2011).

2.3. ERPs

ERPs were assessed using a computerized sequential letter 3-back task (WM) presented in Opensesame version 2.8.3 in Legacy mode and run on the Window XP desktop (Mathôt, Schreij, & Theeuwes, 2012). The stimuli included eight consonant letters (P, B, C, D, J, F, G and H). Vowels were not included in order to prevent syllable creation, with resulting semantic associations or chunking. The letter stimuli were selected to have dissimilar shape features to avoid visual errors due to shape confusions (e.g., V and W; Tsoneva, Baldo, Lema, and Garcia-Molina, 2011). Each letter was randomly shown in white and presented on black background for 500 ms. A fixation dot (●) appeared on the screen between trials (a letter presentation) for 450 ms and the Inter-Stimulus Interval (ISI) was 1000 ms.

Participants were required to press the space bar as fast and as accurately as possible in response to target stimuli. Target trials for the 3-back task (WM) occurred when the presented letter was the same as that presented 3 trials previously (see Fig.1). A main block was preceded by a practice session, which included 24 trials (4 targets). The main blocks for the 3-back task included 160 trials (32 targets). Cognitive performance (mean reaction time and accuracy) on the 3-back task (WM) was also recorded for each stimulus and for the overall task ($\alpha = 0.95$). The mean response accuracy was employed as the primary dependent measure for behavioral data analysis in tandem with other behavioral measures (see section 2.2.1 and 2.2.2).

INSERT FIGURE 1 ABOUT HERE

2.4 Procedures

Following collection of demographic information, the two WASI II subtests were administered, and then the CES and STS tasks (including those during which EEG data was collected), counterbalanced for order. All participants completed the behavioral tasks within 40 minutes.

2.4.1 Electrophysiological acquisition and pre-processing

EEG recordings were conducted continuously from 32 Ag/AgCI scalp electrodes using a NeuroScan Quik-cap designed for a standard international 10–20 system layout (Jasper, 1958). Impedances were maintained below 5 kΩ throughout the recording. The EEG signal was amplified using a NuAmps (40 channels) amplifier and digitized at a sampling rate of 1000 Hz (resampled offline at 250 Hz). A bandpass filter (0.01-100 Hz) was employed prior to digitization and data were filtered offline (1- 40 Hz). During recording, all data were recorded in relation to the virtual ground and re-referenced offline to linked mastoids (A1 and A2).

Horizontal (EOGh; electrodes placed 1.5 cm lateral to the outer canthus of each eye) and vertical (EOGv; electrodes placed 3 mm above the middle of the left eyebrow and 1.5 cm below the left eye) eye movements were recorded using bipolar channels. Blink–related and horizontal ocular movement artefacts were reduced using Independent Component Analysis (ICA), available in EEGLAB toolbox for MATLAB (Delorme & Makeig, 2004; Dickter & Kieffaber, 2014; Hoffmann & Falkenstein, 2008). In addition, visual inspection of the individual participants' ERPs was conducted to manually screen and remove any epochs with significant residual artefact. Following artefact reduction/removal, epochs of 1000 ms were time-locked to the onset of stimuli, baseline correction (-200 to 0 ms), and averaged,

according to stimulus types (non-target, targets). Mean amplitudes and fractional area latencies for ERP components were calculated across intervals, using ERPLAB (Lopez-Calderon & Luck, 2014). Mean amplitudes and 50% fractional area latencies (FAL) were analyzed at a time window of 150-250 ms for the midline fronto-central (FCz) electrode site for P200 and of 300-450 ms for the midline parietal (Pz) electrode site for P300. These measures (mean amplitude and FAL) are less susceptible to high frequency noise (Dickter & Kieffaber, 2014; Luck, 2014).

2.5 Statistical analysis

IBM Statistical Package for the Social Sciences (SPSS) version 24 (IBM Corp, 2016) was used for initial data analysis. IBM SPSS AMOS version 22 (Arbuckle, 2013) was used for testing a path analysis model.

2.5.1 Behavioral and ERP analysis

For behavioral data, the means and standard deviations of the CES, STS, and WM measures across IQ groups (average, high average, and superior) were derived. Furthermore, one-way ANOVAs using a 90% confidence interval and effect sizes (partial eta squared [η_p^2]) tested for IQ group differences across multiple measures (CES: WCST, Flanker, and Alpha span; 3-back task; and STS: digit span and Corsi block). Significant main effects were followed up by post-hoc tests using the Games-Howell correction for equal variances not assumed (Howell, 2010). Only the measures with significant differences between IQ groups were included in the SEM analyses.

For ERPs, in a similar fashion to the behavioral data analysis, the means and standard deviations of non-targets and targets from the 3-back tasks (WM) were considered. One-way

ANOVAs with 90% confidence interval and effect size (η_p^2) were again used to determine the IQ group differences in P200 and P300 mean amplitudes and fractional area latencies for non-target and target conditions. The significant main effects of IQ group were followed up by the Games-Howell correction for equal variances not assumed. (Howell, 2010). Likewise, only the ERP components from the 3-back WM task (P200/300 amplitudes and latencies for non-target and target stimuli) that showed significant differences between the IQ groups were incorporated into the SEM analyses. The ERP components were then used alongside the data from the behavioral measures (WM; CES: Inhibition, updating, and shifting; STS: Verbal and visuo-spatial memory) in statistical analyses predicting *g*, *gC*, and *gF*. The ERP components were included as mediators in the SEM analyses.

2.5.2 SEM analysis of the relation between the different components of WM, ERP measured brain activity and *g*

The Pearson's product–moment correlation coefficient tested for relationships among measures and indicators of the behavioral constructs and ERPs. SEM was used to test the associations between the behavioral and electrophysiological data (Kaplan, 2000), with various goodness-of-fit tests employed to evaluate how well the model or proposed theory fitted the data (Hooper, Coughlan, & Mullen, 2008). These tests were as follows: i) the lower value of a Chi-square test and insignificant p-value (p >0.05) were used to determine whether there was a good model fit (Barrett, 2007); ii) the values of goodness-of-fit statistic (GFI), the adjusted goodness-of-fit statistic (AGFI), the comparative fit index (CFI), and the normed-fit index (NFI) were calculated, their values ranging between 0 and 1; it is widely accepted that the values of 0.90 or higher demonstrate better fitting models (Hu & Bentler, 1999; Kline, 2005; Tabachnick & Fidell, 2007); and iii) the cut-off value for the Root Mean

Square Error of Approximation (RMSEA) was used, with the general consensus that values below 0.05 indicated a good fit (Steiger, 2007).

3. Results

3.1 Behavioral and ERPs

Fig. 2 shows the ERP waveforms and mean amplitudes in response to non-target and target stimuli at the FCz and Pz electrode sites and also the topographic head maps for non-target and target conditions from the 3-back WM task. Overall, at the time window of 175-225 ms, the P200 was fronto-central and dominant at the midline. There was no difference between non-target and target conditions in general. The P300 at the time window of 300-400 ms showed a bilateral distribution with a centro-parietal maximum. There were no particular differences between non-target and target stimuli in the 3-back WM task.

INSERT FIGURE 2 ABOUT HERE

Behavioral performances for the three IQ groups are presented in Table 1, indicating that the superior IQ group produced a higher score than the scores of other IQ groups on all CES, STS, and WM measures. Likewise, the superior IQ group had lower error responses on the WCST than other IQ groups. Furthermore, there were significant differences among the IQ groups on the CES and WM measures: Flanker [$F(2,115) = 11.78$, $p<0.01$, $\eta_p^2 = 0.17$], Alpha [$F(2,115) = 11.55$, $p<0.01$, $\eta_p^2 = 0.17$], WCST [$F(2,115) = 6.06$, $p<0.01$, $\eta_p^2 = 0.10$], and WM [$F(2,115) = 11.48$, $p<0.01$, $\eta_p^2 = 0.17$]. Nevertheless, the IQ group effect failed to reach formal significance on the STS measures: Digit span [$F(2,115) = 2.91$, $p = 0.06$, $\eta_p^2 = 0.05$] and Corsi block [$F(2,115) = 2.87$, $p = 0.06$, $\eta_p^2 = 0.05$].

Table 2 and Figure 3 and 4 show the mean and standard deviation scores of P200 and P300 amplitudes and latencies for both non-target and target conditions from the 3-back WM task. Although the means varied somewhat for the three IQ groups on all ERP components and conditions, there were significant effects only for the P200 latency for target stimuli (P200LT) at FCz [$F(2,115) = 3.93$, $p = 0.02$, $\eta_p^2 = 0.07$], the P300 mean amplitude for non-target stimuli (P300AN) at Pz [$F(2,115) = 5.13$, $p = 0.01$, $\eta_p^2 = 0.08$], and the P300 mean amplitude for target stimuli (P300AT) at Pz [$F(2,115) = 10.92$, $p < 0.01$, $\eta_p^2 = 0.16$].

In summary, a significant association was seen between *g* and performance on CES and WM tasks. Thus, CES functions (shifting, inhibition, and updating) as indexed by WCST, Flanker, and Alpha span tasks respectively were further incorporated to the SEM model for WM–*g* relation as predictors. In addition, the WM construct as indexed by the 3-back task was included in the SEM model as a behavioral mediator. Finally, given the ERP results demonstrated that the P200LT at FCz, P300AN and P300AT at Pz significantly differed across IQ groups, these three ERP components were also included as neurocognitive mediators.

INSERT TABLES 1 AND 2 ABOUT HERE

INSERT FIGURES 3 AND 4 ABOUT HERE

3.2 SEM analysis of the CES of WM and *g* relationships with behavior-ERP data as mediators.

Table 3 shows the correlation coefficients within and among predictors (WCST, Flanker, and Alpha), mediators (P200LT, P300AN, and P300AT), and outcome variables (*gC* and *gF*). The

results indicate multidimensional relationships among specific CES measures. WCST, Flanker, and Alpha span were significantly correlated with each other (*r*'s ranged from 0.23 to -0.32). Significant correlation coefficients among ERP components were observed as well (*r*'s ranged from 0.25 to 0.48). Moreover, significant relationships among WM, CES measures (Flanker and Alpha span) (r = 0.24 and 0.47), and ERP components (r = -0.19, -0.28, and -0.43) were also evident. Additionally, the 3-back WM task had the strongest correlation with *gF* (r = 0.53), followed by WM task with *gC* (r = 0.52), and P300AT with *gC* (r = 0.50).

The SEM is presented in Figure 5, modelling the prediction of *g* by behavioral measures of CES and mediation by WM related ERP components. This model is constructed on the basis that the CES functions of WM moderately correlate with each other and these, in turn, have direct associations with *g*, but are also mediated by neural activity as measured using ERP recording. All goodness-of-fit indices were within acceptable ranges (Kenny, 2015), provided statistical evidence that the postulated model fitted with empirical data. Based on standardized regression coefficients, updating (Alpha span; β = 0.34, p<0.01), inhibition (Flanker; β = 0.21, p<0.01) functions of CES and WM (3-back; β = 0.20, p<0.01) significantly predicted *g*; however, shifting (WCST; β = -0.02, p = 0.81) did not achieve statistical significance. For electrophysiological variables, only the P300AT at Pz (β = -0.31, p<0.01) significantly predicted *g*; the P200LT at FCz and the P300AN at Pz did not (P200LT: β = -0.01, p = 0.98; P300AN: β = -0.01, p = 0.94).

Finally, only the updating and inhibition functions of WM had significant direct and indirect (via the P300AT at Pz as the neuronal mediator and the WM as the behavioral mediator) relationships with *g*. Overall, the CES functions explained 15.1% of the variance in the P200LT at FCz, 23.3% of the variance in the P300AN at Pz, 22.2% of the variance in the P300AT at

Pz and 24% of the variance in WM. Moreover, all CES functions of WM explained 60.4% variance of *g*, 65.7% variance of *gC*, and 62.7% variance of *gF*.

INSERT TABLE 3 AND 4 AND FIGURES 5 ABOUT HERE

4. Discussion

The current study provides novel insight into the ongoing debate regarding the contribution of WM to general cognitive ability (Conway & Getz, 2010; Dahlin, Neely, Larsson, Bäckman, & Nyberg, 2008; Nisbett et al., 2012) by examining the relationship among WM functions and *g*, using behavioral measures (CES, STS, and WM) and ERPs (P200/300 during the 3-back task) The advantage of using SEM was to identify shared variance, more direct associations and mediating effects.

CES measures (switching, inhibition, updating) were interrelated, as were the STS measures, supporting differentiation of EF constructs (Friedman et al., 2006; Miyake & Friedman, 2012; Miyake et al., 2000). Updating was inversely related to P300AN and P300AT, that is, more updating ability was reflected in a decreased P300 amplitude to non-target and target stimuli. Inhibition was inversely associated with P300AT, that is, more inhibitory ability was reflected in a reduced amplitude of P300 component to targets. Whilst, shifting was negatively related to P2LT, that is, more shifting ability was reflected in a reduced latency of P200 component to targets. Inhibition, updating, WM, and P300AT had direct associations with *g*. Thus, current results support WM as a multidimensional construct with interrelated, but distinguishable, functions that relies on a distributed cerebral network, in line with previous behavioral and brain imaging studies that distinguish CES functions (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; Collette & Van der Linden, 2002).

In interpreting this pattern of associations, the theoretical accounts of WM and *g* (Friedman et al., 2006; Kane et al., 2004) may be considered. These authors based their theories on a set of studies that tied together WM capacity, *gF*, and executive attention constructs. They pointed out the central role of controlled attention in sustaining attention in the face of interference or distraction, this being explicitly related to intelligence, and not being related to storage *per se* (Conway, Cowan, Bunting, Therriault, & Minkoff, 2002; Engle et al., 1999). Engle (2018) further emphasized better CES mechanisms in individuals with high *g* in comparison to individuals with low *g*. Namely, high *g* individuals may engage more in problem solving in which they entertain hypothesized solutions, but if ineffective, will readily test novel ideas. In contrast, low *g* individuals are much more likely to re-retrieve ineffective or less successful hypotheses. Current findings suggest that this shifting ability is associated with earlier processing, and its association with *g* is fully explained by inhibition and updating capacity.

Specifically, WM and STS are further explained as distinct processes in this context, albeit substantially correlated. In conditions with high attentional distraction, WM task performance relies much more on the CES or controlled attention than STS (Engle et al., 1999) in terms of sustained internal attention across multiple stages of prioritizing information in WM (Myers et al., 2017). In addition, STS capacity in humans has been increased within a narrow range for a hundred years (Gignac, 2015; Wongupparaj, Wongupparaj, Kumari, & Morris, 2017) and a recent study has found an important role of CES on information manipulation and compression to achieve lower memory demands to solve new problems (Mustapha, Nicolas, Alessandro, & Fabien, 2018).

The P200 and P300 appear to reflect distinct CES processes, at pre- and post-perceptual stages, during the 3-back task performance. Whilst less is known about the functional significance of the P200 compared to an extensive literature on P300, it has been proposed as reflecting processes underpinning perceptual matching and stimulus classification, such as stimulus detection, evaluation, storage, and encoding (Crowley & Colrain, 2004; Gholami Doborjeh, Kasabov, Gholami Doborjeh, & Sumich, 2018; Potts, 2004) that facilitate the post-perceptual processing as reflected by the P300 wave (Chen et al., 2008). Other studies have implicated P200 mechanisms in stimulus switching (Karayanidis & Michie, 1997; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Stefanics, Kremláček, & Czigler, 2014). The current findings linking P200 latency with WCST switching are in line with these ideas. WCST switching relies on cognitive matching, with better scores reflecting the ability to change problem-solving strategies to match rules (Nyhus & Barceló, 2009).

A large body of literature has associated P300 with WM processes (Fabiani, Karis, & Donchin, 1986; Kok, 2001; Morgan, Klein, Boehm, Shapiro, & Linden, 2008; Polich, Howard, & Starr, 1983; Saliasi et al., 2013). For this reason, it was anticipated that P300 would be associated with both CES and STS. Other authors have similarly reported a null relationship between P300 and STS (Chapman, Gardner, Mapstone, Dupree, & Antonsdottir, 2015; Danker et al., 2008). However, using SEM in the current study has allowed identification of a more specific role for P300 in the CES, in particular, updating and inhibition/cognitive control, at least in young adults. Thus, P300 amplitude appears to index WM comparisons, namely, it involves interference control and removal, stimulus active manipulation, and updating processes that link with encoding operations to facilitate subsequent access of the remembered material (Chen, Mitra, & Schlaghecken, 2008; Polish, 2012; Singh, Gignac, Brydges, & Ecker, 2018; Vilà-Balló et al., 2018).

Findings for P300 contrast studies showing positive relationships between the P300 amplitude and *gF* (e.g., during a hybrid mental/rotation/Go-NoGo task; Varriale, van der Molen, & De Pascalis, 2018), but rather support the neural efficiency theory that proposes reports of lower activity in higher functioning participants reflect more efficient processing (Dunst et al., 2014; Graham et al., 2010). Thus, the current findings might be explained by assuming that high-ability individuals have a more efficient use of brain resources (shorter P200 latency and lower P300 amplitude) in terms of interference control and active maintenance during WM updating processes. In line with this, overall response accuracy for high average and superior IQ individuals on the 3-back task was approximately 86%, suggesting it was completed with less effort. Future studies should investigate more challenging tasks that might require greater resource allocation from high and superior IQ individuals.

In light of the neural efficiency model it should be noted that the current sample had a relatively higher than average IQ (~115), thus results might not be generalizable to lower IQ or cognitively impaired groups. Future studies should apply the current model to a wider demographic and socio-economic characteristics. The current data do not support previous reports of an association between STS and *g* (Colom, Abad, Rebollo, & Chun Shih, 2005; Colom, Flores-Mendoza, Quiroga, & Privado, 2005; Oberauer, Schulze, Wilhelm, & Süß, 2005). This could be due to differences between studies in how the STS is operationalized. For example, Colom et al (2005) used a more extensive battery to assess STS, including forward and backward span tasks for letters and digits, as well as Corsi's block span and the dot memory tasks, which might recruit attentional control from CES as well. Due to the time-consuming behavioral task administration and EEG recording of the current study, we restricted the number of behavioral tasks used to measure both the CES and STS. Forward digit span may

suffer from limited range in the current sample, given that approximately 90% of the healthy adults are able to recall somewhere between five and eight digits (Wechsler, 1939) ($M_{current\ study}$=7.21)

The Corsi's block span task used in the current study might also have been prone to ceiling effects, given that a time constraint was not used. According to the time-based resource-sharing model (Barrouillet & Camos, 2007), it is possible that the time constraints do not substantially affect WM capacity. The amount of time in which items are attended to may be sufficient to refresh or rehearse the relevant memory traces; the maintenance processes may not compete with control system (CES) sharing limited resources in comparison to CES tasks that are required to respond immediately. This is in line with the notions that simple span tasks can sometimes correlate with measures of *gF*, if the stimuli are very rapidly presented to participants and they are presented with long lists of items (Conway, Getz, Macnamara, & Engel de Abreu, 2011).

In conclusion, the current study draws on the strengths of SEM to offer novel insight for understanding brain processes underpinning the relationship between WM and *g*. Findings have important implications for understanding *g* and cognitive processes reflected in P200 and P300 ERP components. They suggest that mechanisms within the P200 time-window are involved in shifting attention, whilst P300 is more associated with CES (inhibition and updating). *g* is best predicted by inhibitory and updating functions of CES, with additional independent contributions from WM (behavioral) and parietal P300 measures.

Conflict of Interest

The authors declare no conflict of interest.

Contributors

Peera Wongupparaj, Alexander Sumich, Veena Kumari and Robin G. Morris designed the study. Megan Wickens was partially responsible for recruiting participants and recording brain waves. Peera Wongupparaj undertook the statistical analysis and prepared the first draft. All authors contributed to and approved the final manuscript.

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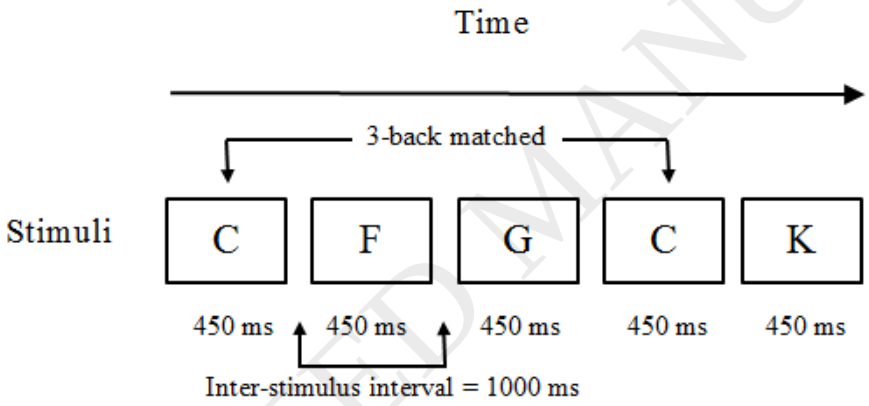
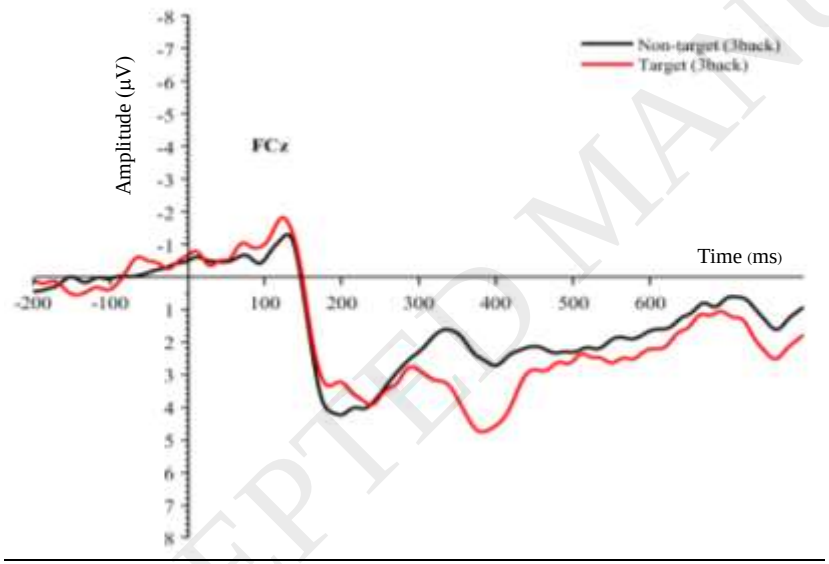
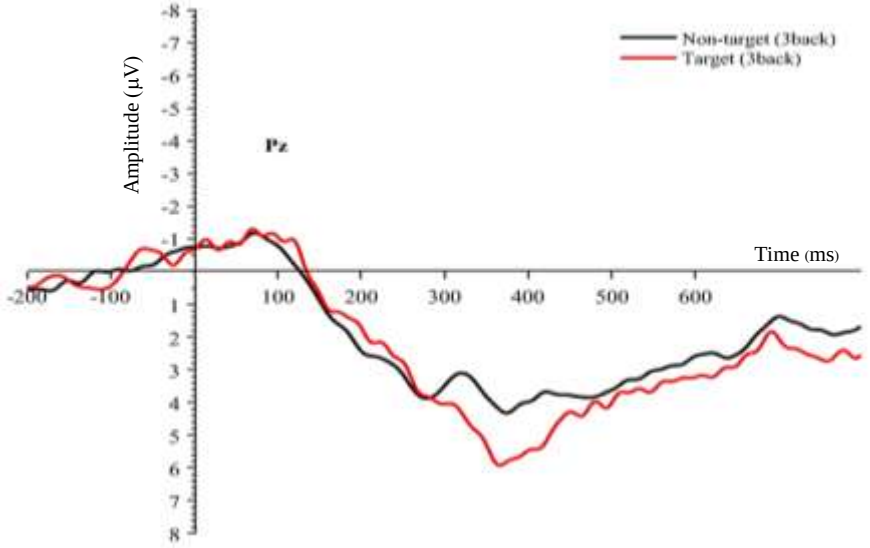


Fig. 1. Experimental paradigm showing the timing for the 3-back task.





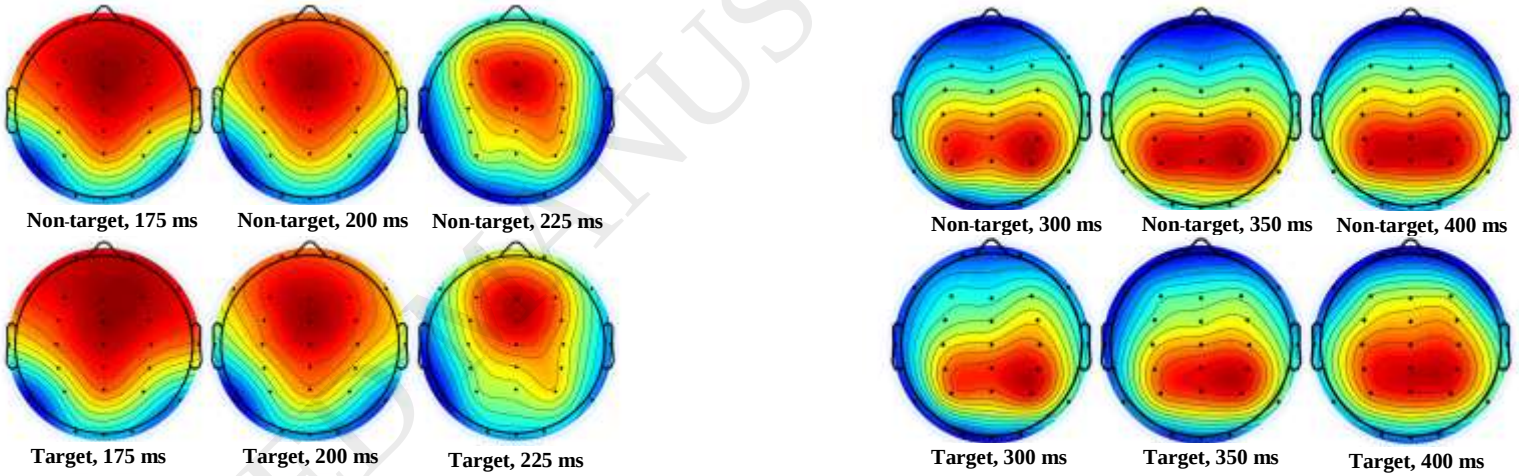


Fig. 2. Grand mean ERP waveforms for non-target stimuli (NTS, **Black line**) and target stimuli (TS, **Red line**) at the FCz and Pz electrode sites. 2D-topographical distributions are shown for the grand average across conditions (non-target and stimuli) and timing (P200: 175, 200, and 225 ms and P300: 300, 350, and 400 ms) for the 3-back WM task.

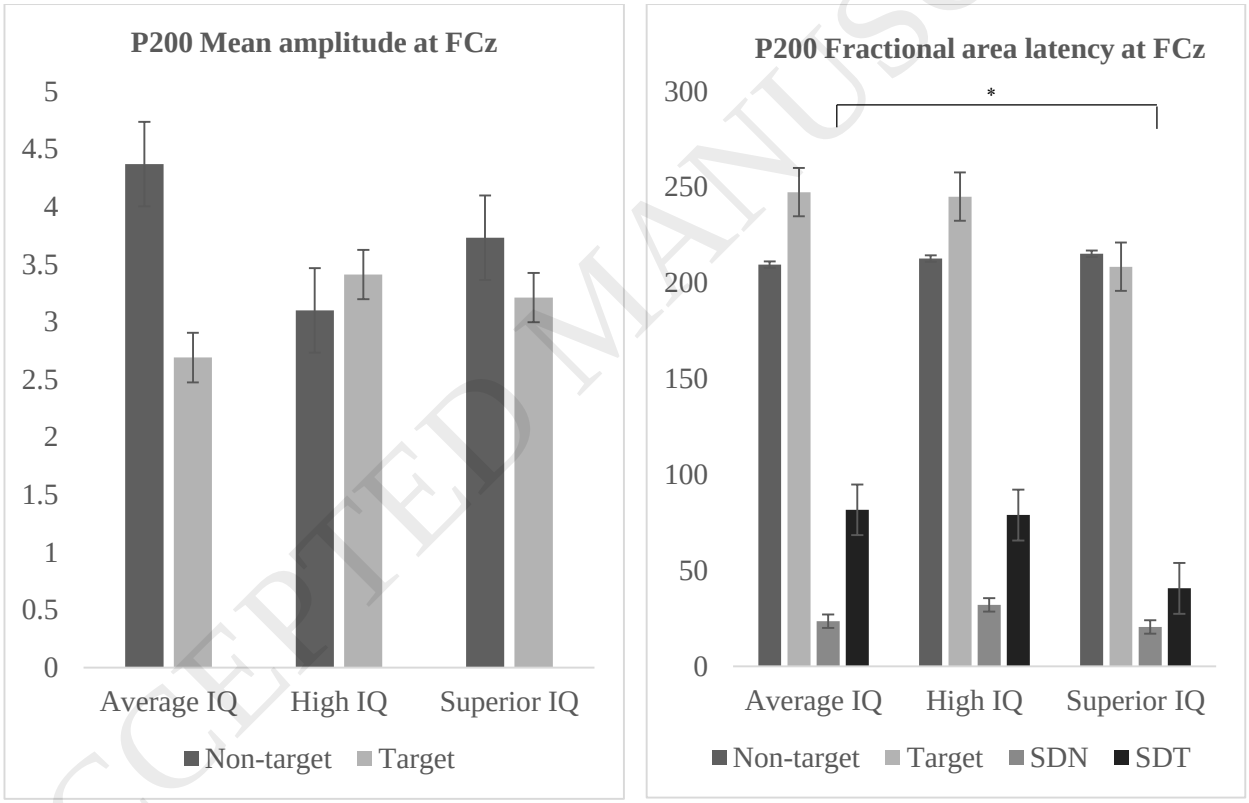


Fig. 3. Grand mean P200 mean amplitude and fractional area latency for non-target and target stimuli of the 3-back WM task, categorized by IQ groups.

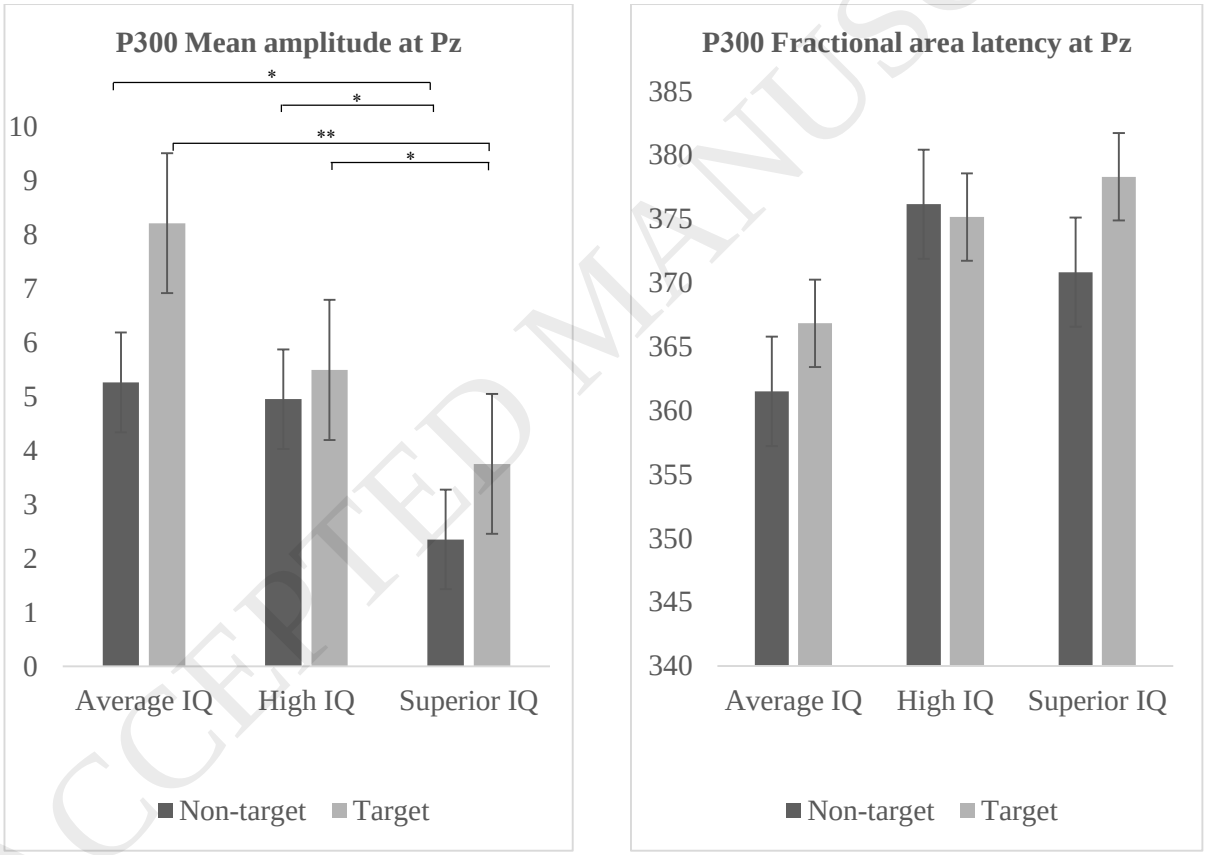


Fig. 4. Grand mean P300 mean amplitude and fractional area latency for non-target and target stimuli of the 3-back WM task, categorized by IQ groups.

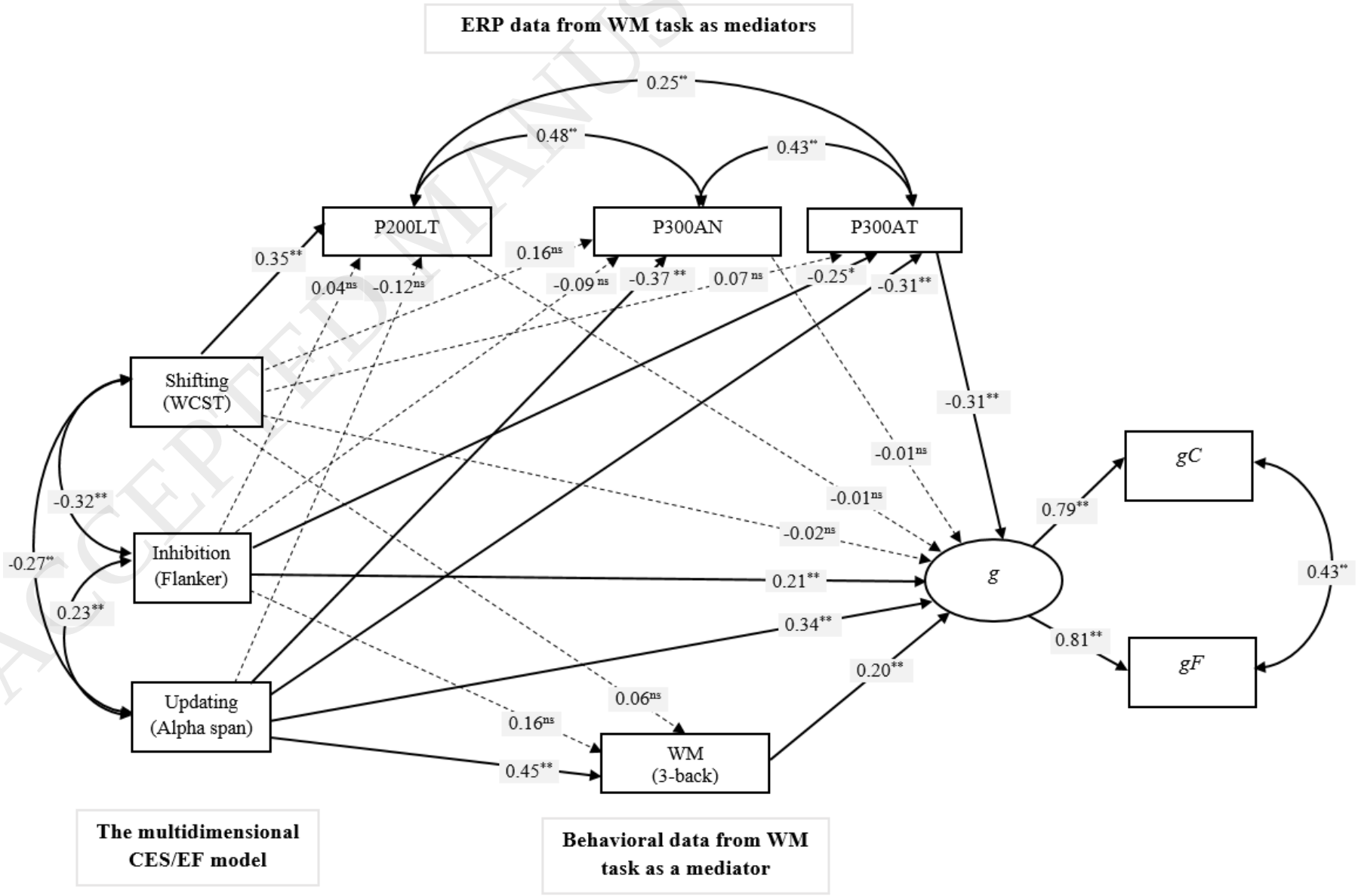


Fig. 5. SEM relating the CES of a multicomponent WM (CES: Shifting, inhibition, and updating) to *g*, mediated by the $P300_{3back\text{-}WM}$ mean amplitude for target stimuli (P300AT) at Pz electrode site (N=115) (Chi-square, *df* = 13.17, 10, *p* = 0.21/ GFI = 0.97/ AGFI = 0.89/ CFI = 0.99/ NFI = 0.96/ RMSEA 0.05). (Dashed lines represents non-significant paths; ns = non-significant; ** = $p<0.01$; *=$p<0.05$).

Table 1. Means, standard deviations, and the effects of IQ group on the behavioral tasks.

Task	Mean (SD)			F (df_1, $_2$)	η_p^2
	Average	High average	Superior		
Flanker	**92.10 (4.56)**	**95.72 (4.34)**	**96.26 (3.54)**	**11.78 (2,115)****	**0.17**
Alpha	**62.76 (7.95)**	**65.56 (6.35)**	**70.67 (7.88)**	**11.55 (2.115)****	**0.17**
WCST	**16.95 (7.41)**	**14.26 (7.08)**	**11.85 (5.11)**	**6.06 (2,115)****	**0.10**
WM[1]	**83.31 (3.88)**	**85.81 (3.80)**	**88.01 (5.32)**	**11.48 (2,115)****	**0.17**
Digit	6.85 (1.35)	7.32 (1.17)	7.48 (1.06)	2.91 (2,115)^{ns}	0.05
Corsi	62.44 (22.17)	64.65 (24.49)	74.58 (25.57)	2.87 (2,115)^{ns}	0.05

Note [1]3-back WM task; ns = non-significant, *$p<0.05$, **$p<0.01$; $N_{Average\ ,\ High\ average,\ Superior}$ $=41, 34, \& 40$.

Table 2. Means, standard deviations, and the effects of IQ group for the P200 and P300 mean amplitude and fractional area latency for non-target and target stimuli of 3-back WM task (electrophysiological task).

Effect	Mean (SD)			F (df_1, df_2)	η_p^2
	Average	High average	Superior		
P200 mean amplitude for non-target stimuli (P200AN) at FCz	4.37 (3.30)	3.10 (3.10)	3.73 (2.71)	1.61 (2,115)^{ns}	0.03
P200 mean amplitude for target stimuli (P200AT) at FCz	2.69 (3.30)	3.41 (3.14)	3.21 (2.90)	0.55 (2,115)^{ns}	0.01
P200 fractional area latency for non-target stimuli (P200LN) at FCz	209.54 (23.49)	212.78 (32.01)	215.26 (20.46)	0.52 (2.115)^{ns}	0.01
P200 fractional area latency for target stimuli (P200LT) at FCz	**247.42 (81.62)**	**245.02 (78.87)**	**208.43 (40.61)**	**3.93 (2,115)***	**0.07**
P300 mean amplitude for non-target stimuli (P300AN) at Pz	**5.26 (4.24)**	**4.95 (4.41)**	**2.35 (4.64)**	**5.13 (2,115)****	**0.08**
P300 mean amplitude for target stimuli (P300AT) at Pz	**8.21 (3.90)**	**5.49 (3.85)**	**3.75 (5.07)**	**10.92 (2,115)****	**0.16**
P300 fractional area latency for non-target stimuli (P300LN) at Pz	361.51 (35.39)	376.16 (36.91)	370.84 (36.50)	1.59 (2,115)^{ns}	0.03
P300 fractional area latency for target stimuli (P300LT) at Pz	366.84 (25.10)	375.16 (34.38)	378.31 (26.35)	1.74 (2,115)^{ns}	0.03

Note ns = non-significant, *$p<0.05$, **$p<0.01$; $N_{Average\ ,\ High\ average,\ Superior\ IQs}$ $=41, 34, \& 40$.

Table 3. Descriptive statistics and correlation coefficients between measures used in the SEM for cognitive-behavioral-electrophysiological model of WM-*g* relations (N=115).

Measures	**Mean (SD)**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1. WCST[a]	14.38 (6.88)	1.00								
2. Flanker[a]	94.62 (4.54)	-0.32**	1.00							
3. Alpha$_a$	66.34 (8.15)	-0.27**	0.23**	1.00						
4. WM[a]	85.69 (4.80)	-0.11^{ns}	0.24**	0.47**	1.00					
5. P200LT[b]	233.15 (70.94)	-0.37**	-0.10^{ns}	0.21*	-0.19*	1.00				
6. P300AN[b]	4.16 (4.59)	-0.29**	-0.23*	-0.44**	-0.28**	0.48**	1.00			
7. P300AT[b]	5.86 (4.69)	-0.24**	-0.35**	-0.38**	-0.43**	0.25**	-0.43*	1.00		
8. *gC*[a]	58.44 (6.57)	-0.21*	0.31**	0.44**	0.52**	-0.18^{ns}	-0.36**	-0.50**	1.00	
9. *gF*[a]	57.07 (7.69)	-0.23*	0.41**	0.43**	0.53**	-0.17^{ns}	-0.28**	-0.48**	0.64**	1.00

Note [a] = Behavioral data, [b] = ERP data, ns = non-significant, *$p<0.05$,**$p<0.01$.